Host fidelity is an effective premating barrier between sympatric races of the apple maggot fly

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ABSTRACT   Models of sympatric speciation for phytophagous insects posit a central role for host plant-associated mating as a premating isolating mechanism in lieu of geographic barriers to gene flow. Here, by means of three mark-and-recapture studies, we confirm that host fidelity (i.e., the tendency of an insect to reproduce on the same host species that it used in earlier life-history stages) restricts gene flow between sympatric apple- and hawthorn-infesting races of *Rhagoletis pomonella* (Diptera: Tephritidae) to ≈6% per generation. Genetically based differences in host preference, adult eclosion under the "correct" host species, and allochronic isolation contribute to host fidelity in various degrees in the races. The results verify that host-associated adaptation can produce reproductive isolation as a correlated character (a key premise of sympatric speciation). The study also represents one of the few or perhaps only example in animals where the intra-specific isolating effects of specific phenotypes have been quantified in nature.

Speciation in animals can theoretically occur in sympatry (i.e., in the absence of geographic isolation) if the following series of requirements are met. (*i*) Organisms mate on preferred hosts, with different conspecific subpopulations tending to mate on different hosts (refs. 1 and 2). (Note that although we refer to host-specific taxa, our comments also apply to sympatric divergence based on habitat specialization.) (*ii*) The semiautonomous nature of host-specific subpopulations ("host races") permits the refinement of host-associated adaptations (e.g., traits involved in survivorship or performance on a host) that produce reproductive isolation as a correlated character, by either pleiotropy or negative genetic tradeoffs (3, 4). (*iii*) These host-associated adaptations either isolate the host races to such an extent that they represent distinct species or favor the evolution of additional prezygotic barriers to gene flow that eventually lead to speciation; in the latter case, the additional premating isolation is most likely to involve traits increasing host fidelity, but it could also be caused by the evolution of assortative mating traits not directly tied to host selection (i.e., pheromones, cuticular hydrocarbons, or mating structures).

Allozyme studies suggest that hawthorn (*Crataegus* spp.)- and recently derived apple (*Malus pumila*)-infesting populations of *Rhagoletis pomonella*, the apple maggot fly, represent host races in the initial stage of sympatric divergence (5–7). Because these flies mate exclusively on or near the fruit of their host plants (8, 9), a test for the existence and effectiveness of host fidelity (the tendency of an insect to reproduce on the same host species that it used in earlier life-history stages) as a premating isolating mechanism is possible (requirement *i* for sympatric speciation). Here, by means of three mark-and-recapture studies conducted at a
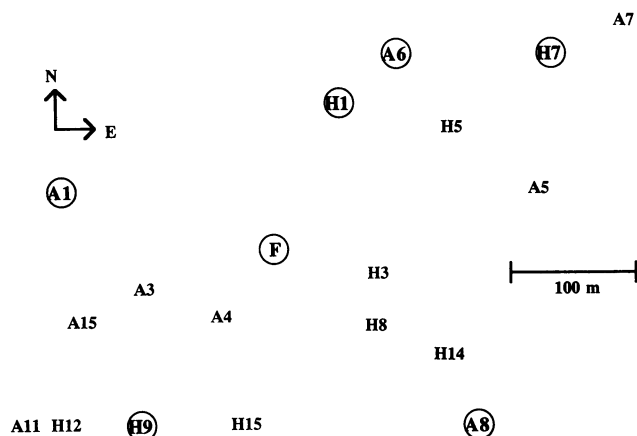
FIG. 1. Diagram of the Grant, Michigan, study site. Apple (A) and Hawthorn (H) trees sampled in the study are given along with their numerical designations. Release trees and release point F are circled.

study site near Grant, Michigan (Fig. 1), we verify that host fidelity is fairly strong in *R. pomonella*, restricting genetic exchange between apple- and hawthorn-infesting races to ≈6% per generation per year (*R. pomonella* are univoltine).

At least three factors may contribute to host fidelity in *R. pomonella*. The first factor is genetically based differences in host preference. Previous studies have shown that *R. pomonella* adults mate exclusively on or near the fruit of their host plants (8, 9). Therefore, genetically based traits increasing the preference of flies for either apples or hawthorns could establish a system of positive assortative mating based on host choice.

A second factor affecting host fidelity relates to the host species beneath which an adult fly ecloses. If adults are sedentary and tend to remain in the area where they eclose, then the local composition of host plant species could influence host use by flies. In addition, apple-origin females can be trained through repeated exposure to either apples or hawthorns to defer from ovipositing into the alternative, unfamiliar host fruit (10). Therefore, adults may be conditioned to disproportionately utilize the host species that they first encounter after eclosing. Conditioning in fly larvae is extremely unlikely, however, as the "Hopkins Host Selection Principle" has never been demonstrated for any phytophagous insect, including *R. pomonella* (11–14).

The third factor potentially involved in host fidelity is seasonal isolation (allochrony) due to host-associated differences in the timing of adult eclosion. Previous studies have shown that apple-infesting flies eclose significantly earlier than hawthorn-infesting flies when reared under both laboratory and field conditions and that this difference is genet-

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ically based (15, 16). Because adult longevity is limited and fruit of apple varieties favored by *R. pomonella* ripen ≈3 weeks earlier than those of hawthorns, eclosion time differences may limit the opportunity for apple- and hawthorn-origin flies to use alternative host species.

MATERIALS AND METHODS

The three mark-and-recapture experiments reported in this manuscript were designed to partition host fidelity in *R. pomonella* into its primary components of host preference, eclosion under the "correct" host species, and seasonal isolation. These three experiments are designated the field-release study, the host-switch study, and the net-release study, respectively.

Field-Release Experiment. The rationale behind the field-release experiment was to release "naive" apple- and hawthorn-origin flies in the middle of our study site under neither host species (see F in Fig. 1) and examine their subsequent distributions on apple and hawthorn trees. In principle, this provides an estimate of how flies would assort themselves based solely on genetic differences in host preference.

Flies used in the field-release experiment were collected as larvae in infested fruit at the Grant site in the summer of 1991 and allowed to pupate in moist vermiculite. We sifted pupae from the vermiculite, placed them in Petri dishes, and stored the Petri dishes at 4°C in a refrigerator to simulate overwintering conditions. We removed the Petri dishes from the cold at various times during the 1992 field season and put them in Plexiglas cages at room temperature, with each race having its own set of cages. Newly eclosing, "naive" flies were marked and released as quickly as possible in the middle of the study site under neither host species (see F in Fig. 1). We chose the field-release point to be as equidistant as possible to the same number of apple and hawthorn trees. To control against the possible effects of prolonged cage-rearing on host preference, we periodically emptied the Plexiglas cages to ensure that all released flies were younger than 5 days old. Marking consisted of coloring a fly's notum with liquid correction fluid (point F and each of the release trees in the other two experiments being distinguished by a different color) and drawing a symbol (representing one of eight different release periods; see Tables 1 and 2) on the dried fluid in either black (for apple-origin flies) or red (hawthorn-origin

flies) with a permanent marker. We released flies in the late afternoon during the indicated periods in Tables 1 and 2 and collected them by using mouth aspirators no sooner than 16 hr later over the next 2–4 days. Recaptured flies were marked on their wings and rereleased at the point of their capture at the start of the next release period. Data presented in this report are for first-time recapture flies only. Inclusion of multiple recapture flies had little effect on any of the calculated values of host fidelity.

The rearing scheme we used in the field-release study allowed us to release large numbers of apple (*n* = 1082)- and hawthorn (*n* = 1325)-origin flies throughout the season. This eliminated the effect of allochronic isolation. Because we released flies in the middle of our study site, we could also factor out eclosing under the "correct" host species, leaving genetically based differences in host preference as the primary factor determining host fidelity in the field-release experiment.

Host-Switch Experiment. In the host-switch experiment, we released adults of both races under their own and the other race's host trees. We then compared recapture frequencies of the races on the host trees under which they were released ("release trees") as a second test for genetically based differences in host preference.

Flies used in the host-switch study were reared in the same manner and released according to the same schedule as those in the field-release experiment. But instead of releasing adults in the middle of the study site, we released both apple- and hawthorn-origin flies under apple trees 1, 6, and 8 and hawthorn trees 1, 7, and 9 (see Tables 1 and 2 for release numbers schedules).

Net-Release Experiment. The goal of the net-release experiment was to determine overall levels of host fidelity for *R. pomonella* taking into account all factors potentially affecting host fidelity, including allochronic isolation.

We captured newly eclosing "naive" adults in ground traps ("nets") beneath host trees in both 1991 and 1992, marked, and released them. Therefore, the 1991 and 1992 net experiments paralleled the natural eclosion patterns of the races in both the timing and density of fly release. We marked "net flies" in the same way that we did "host-switch flies," except that we also colored the scutellar dots of net flies. In 1992, we released almost exactly equal numbers of marked apple-origin net flies under apple trees 1, 6, and 8 (total *n* for all

Table 1. First-time recapture data from the host switch experiment for apple release trees 1, 6, and 8

| Symbol | Month/day period | | Sample time,* min × 10⁻⁴ | Ap.-origin flies | | Haw-origin flies | | Freq. recapt. ratio Ap.-origin/total flies[†] |
	Release	Sampling		No. rel.	Freq. recapt.	No. rel.	Freq. recapt.	
..	7/2–5	7/6	1.07 (1.15)	189	0.180	181	0.083	0.684 (*P* = 0.0086)
|	7/7–10	7/13	1.03 (1.10)	217	0.249	462	0.054	0.821 (*P* < 0.0001)
+	7/14	7/15–17	1.02 (1.09)	141	0.305	330	0.058	0.841 (*P* < 0.0001)
∧	7/17–18	7/20–21	0.96 (1.03)	177	0.215	135	0.111	0.659 (*P* = 0.0218)
−	7/22–23	7/24–28	0.83 (0.89)	327	0.180	320	0.088	0.673 (*P* = 0.0005)
·	7/29–30	7/31, 8/4–6	0.69 (0.73)	343	0.172	362	0.061	0.739 (*P* < 0.0001)
:	8/7–10	8/11–14	0.53 (0.56)	260	0.112	350	0.037	0.750 (*P* = 0.0005)
∴	8/14–15	8/16–9/20	0.26 (0.28)	494	0.085	468	0.056	0.605 (*P* = 0.0791)
	Host-switch total[‡] (Ap. trees)			2148	0.167	2608	0.062	0.722 (*P* < 0.0001)[§]

Ap., apple; Haw, hawthorn; Freq. recapt., frequency of recapture; No. rel., number released.
*Numbers not in parentheses are the collecting times in min × 10⁻⁴ for apple release trees 1, 6, and 8. Numbers in parentheses are the collecting times for all apple trees at the Grant site.
[†]Probability levels for the eight individual release period tests of recapture frequency ratio of apple-origin/total flies were determined by Fisher's exact tests of 2 × 2 tables of frequencies of recaptured and nonrecaptured apple- and hawthorn-origin flies.
[‡]For the "Host-switch total" row, the frequencies of recapture for apple- and hawthorn-origin flies are given in relation to the total number of flies released. However, the final apple-origin fly/total fly recapture frequency ratio (0.722) is the average of the ratio values across the eight release periods (symbols). This latter value is more appropriate than calculations based on the total recapture data because it accounts for differences in the ratios and numbers of apple- and hawthorn-origin flies released across the eight periods.
[§]Probability levels for host-switch and field-study totals were determined by Fisher's method of combining probabilities (17) applied across the eight individual release period tests. In Table 2, when the recapture frequency ratio of hawthorn-origin/total flies was <0.5, we calculated 2 lnP instead of −2 lnP.

Table 2.   First-time recapture data from the host switch experiment for hawthorn release trees 1, 7, and 9

Symbol	Month/day period		Sample time,* min × 10⁻⁴	Ap.-origin flies		Haw-origin flies		Freq. recapt. ratio Haw-origin/total flies†
	Release	Sampling		No. rel.	Freq. recapt.	No. rel.	Freq. recapt.	
..	7/2–5	7/6	1.07 (1.15)	192	0.052	188	0.117	0.692 (P = 0.0227)
ǀ	7/7–10	7/13	1.03 (1.10)	220	0.041	449	0.062	0.604 (P = 0.2851)
+	7/14	7/15–17	1.02 (1.09)	136	0.118	332	0.105	0.473 (P = 0.7743)
∧	7/17–18	7/20–21	0.96 (1.03)	168	0.095	129	0.093	0.494 (P = 1.0000)
–	7/22–23	7/24–28	0.83 (0.89)	314	0.086	319	0.129	0.599 (P = 0.0954)
·	7/29–30	7/31, 8/4–6	0.69 (0.73)	334	0.159	360	0.117	0.424 (P = 0.1219)
:	8/7–10	8/11–14	0.53 (0.56)	273	0.158	348	0.141	0.472 (P = 0.5711)
∴	8/14–15	8/16–9/20	0.26 (0.28)	491	0.102	478	0.109	0.517 (P = 0.7541)
		Host-switch total‡ (Haw trees)		2128	0.105	2603	0.108	0.534 (P > 0.7500)§

Ap., apple; Haw, hawthorn; Freq. recapt., frequency of recapture; No. rel., number released.
*,†,‡,§Footnotes are the same as in Table 1, except that they apply to hawthorn rather than apple release trees.

three apple trees = 424) and hawthorn-origin net flies under hawthorn trees 1, 7, and 9 (total n = 362). Additional apple (trees 5 and 11) and hawthorn (tree 8) release trees were used in the 1991 net study, and only flies emerging from beneath a tree were released under that tree. A total of 348 apple-origin net flies and 312 hawthorn-origin net flies were released in 1991.

RESULTS AND DISCUSSION

The field-release experiment assessed whether innate host preference differences exist between populations of apple- and hawthorn-origin flies. An average of 93.7% of flies recaptured on apple trees across the eight release periods in the field-release experiment were apple-origin flies (93.7% represents the average across the eight release periods of the percentage of marked field-release flies recaptured on apples that were of apple origin; Table 3). Slightly under 50% of all flies recaptured on hawthorn trees were hawthorn-origin flies (Table 3). These results are suggestive of host-preference differences between the races. However, if marked hawthorn-origin flies emigrated from our field site more frequently than apple-origin flies, then this could also partially account for the observed pattern. To eliminate possible emigration biases, we calculated the relative preference of each race for apple versus hawthorn trees. Relative preferences were calculated separately for each of the eight release periods in the field-release experiment by taking the recapture frequency of a race on its host species of origin and dividing this value by the recapture frequency for the same race on both hosts, with recapture frequencies being weighted by the time spent collecting (sampling duration) on apple and hawthorn trees. Average relative preferences were then calculated as the means of the eight release period estimates. The average relative preference of hawthorn-origin flies for hawthorn over apple trees was 91.2% (χ^2 goodness of fit to 1:1 expected ratio = 51.3, P < 0.0001, 1 df, n = 78). In comparison, the relative preference of apple-origin flies for apple over hawthorn trees was only 55.2% (χ^2

= 1.7, P < 0.10, 1 df, n = 136). Naive apple- and hawthorn-origin flies therefore have different propensities to accept apple and hawthorn trees.

The host-switch experiment provided a second test for innate host preference differences between the races. Here, we released naive apple- and hawthorn-origin adults under their own and the other race's host trees and monitored their subsequent host acceptance behaviors. There was no significant heterogeneity in recapture frequencies of apple- relative to hawthorn-origin flies among either the three apple release trees 1, 6, and 8 or the three hawthorn release trees 1, 7, and 9 (*G*-contingency test among apple trees = 2.36, P = 0.311, 2 df; *G*-contingency test among hawthorn trees = 1.88, P = 0.398, 2 df). We therefore pooled the results across release trees. Apple-origin flies were recaptured on their original apple release trees significantly more often than hawthorn-origin flies for seven of the eight release periods. (Data for each release period were analyzed for statistical significance by Fisher exact tests on 2 × 2 tables of the raw numbers of apple-origin flies recaptured on apple release trees, apple-origin flies not recaptured on apple release trees, hawthorn-origin flies recaptured on apple release trees, and hawthorn-origin flies not recaptured on apple release trees.) The final column in Table 1 (frequency of recapture ratio for apple-origin/total flies) summarizes the results for the apple tree component of the host-switch experiment in the form of a relative recapture measure of apple- to hawthorn-origin flies. These values were calculated separately for each of the eight release periods by dividing the frequency that apple-origin flies were recaptured on apple release trees by the sum of the frequencies that apple- and hawthorn-origin flies were recaptured on apple release trees. Recapture frequencies, rather than raw recapture numbers, had to be used in these estimates because different numbers of apple- and hawthorn-origin flies were released during each of the release periods. Therefore, a value of 0.5 would indicate that if an equal number of apple- and hawthorn-origin flies were released in a given period under an apple release tree, then they would be equally likely to be recaptured on that tree. An average of

Table 3.   First-time recapture totals for apple- and hawthorn-origin flies on apple and hawthorn trees in the field-release experiment

Recapture	Ap.-origin flies		Haw-origin flies		Freq. recapt. ratio Ap.-origin/total flies
	No. rel.	Freq. recapt.	No. rel.	Freq. recapt.	
On Ap. trees	1082	0.062	1325	0.008	0.937 (P < 0.0001)*
On Haw trees	1082	0.064	1325	0.051	0.505 (P > 0.9500)*

The frequencies of recapture (Freq. recapt.) for apple (Ap.)-origin and hawthorn (Haw)-origin flies are given in relation to the total number of flies released (No. rel.). However, the frequency recapture ratios of apple-origin/total flies are the averages of the values across the eight release periods. These latter values are more appropriate than calculations based on the total recapture data because they account for differences in the ratios and numbers of apple- and hawthorn-origin flies released across the eight periods.
*Probability levels for the field-release study totals were determined by Fisher's method of combining probabilities (17) applied across the eight individual release period 2 × 2 Fisher exact tests.

72.2% of marked flies recaptured across the eight release periods on apple release trees in the host-switch experiment were apple-origin flies (Table 1). Therefore, apple-origin flies showed a greater propensity to accept apple trees in the host-switch experiment than hawthorn-origin flies ($\approx$2.6:1 ratio). In comparison, apple- and hawthorn-origin flies were recaptured in roughly equivalent proportions on hawthorn release trees (Table 2), much as they were in the field-release experiment.

Data from the host-switch experiment can also be used to derive estimates of host fidelity based on the combined effects of host preference and adult eclosion under the "correct" host species. For the apple-infesting race, this was done by calculating recapture rates of apple-origin flies released under apple trees and recaptured on any apple tree relative to recapture rates of apple-origin flies on either host species. The average host fidelity of apple-origin flies for apple trees was 92.1%. It was 83.3% for hawthorn-origin flies for hawthorn trees.

One concern about the host-switch experiment is whether we disproportionately recaptured marked flies in the collecting periods immediately following their release. If so, then we may have biased our estimates of host preference and fidelity by not giving flies sufficient time to assort themselves on hosts. But the mean number of days from release to first recapture for apple-origin flies on apple release trees was 15.95 $\pm$ 0.60 days ($\pm$SE; $n = 358$), while it was 14.99 $\pm$ 0.94 days ($n = 161$) for hawthorn-origin flies on apples. On hawthorn release trees, first recaptures occurred an average of 10.54 $\pm$ 0.69 days ($n = 224$) after release for apple-origin flies and 12.27 $\pm$ 0.72 days ($n = 281$) for hawthorn-origin flies. We therefore did not simply recapture marked flies immediately after they were released. Rather, sufficient time elapsed between release and recapture for the host-switch data to accurately reflect the degree to which the races accepted and rejected apple and hawthorn trees.

Where did flies go during the time period before we recaptured them? A certain number undoubtedly remained on host trees and evaded recapture. In addition, *R. pomonella* flies are not sexually active immediately after they eclose but require a period of from 7 to 14 days before they reach sexual maturity (8, 9, 18). It is generally thought that immature flies forage through the field, feeding on bird droppings and honey dew on host and nonhost plants, before returning to host plants to mate and oviposit (19). Prokopy *et al.* (8) have reported searching for, but not finding, flies mating off of host plants in the field. We have also looked for flies foraging and mating in the underbrush. However, *R. pomonella* densities were so low off of host plants that we failed to observe any flies in several hours of searching. These findings support the host-specific nature of mating in *R. pomonella*.

The host-switch and field-release experiments strongly suggest that genetically based differences in host preference exist between the races. The only other possibility is preimaginal conditioning, which has never been documented for any phytophagous insects including *R. pomonella* (11–14). Our results show that hawthorn-origin flies have an aversion for apples. Apple-origin flies have overcome this aversion and gained the ability to recognize apples as new hosts—this while retaining their penchant for the ancestral host hawthorn. Prokopy *et al.* (14) observed the same pattern in the oviposition acceptance behavior of naive apple- and hawthorn-origin females in laboratory, single fruit presentation assays.

The net-release experiment was designed to estimate overall levels of host fidelity for *R. pomonella*, taking into account all possible factors affecting host fidelity, including allochronic isolation. In 1992, 43 of 45 recaptured hawthorn-origin "net flies" were collected on hawthorn trees, while 66

of 71 recaptured apple-origin flies were caught on apples. When these data were adjusted for sampling durations on host trees, they translated into a 95.0% level of host fidelity for hawthorn-origin flies for hawthorn trees and a 93.1% level of host fidelity for apple-origin flies for apple trees. Results from the 1991 net study were similar to those from 1992, as 32 of 33 marked hawthorn-origin flies were recaptured on hawthorns (97.1% level of host fidelity) and 67 of 72 marked apple-origin flies were collected on apples (92.8% host fidelity). Overall levels of host fidelity are therefore fairly high in *R. pomonella*, but they are not absolute.

Analyses of the three mark–recapture studies conducted in 1992 let us determine the extent to which host fidelity reduces gene flow between the races and partition host fidelity into its component elements. If we consider genetically based differences in host preference alone and assume an equal number and temporal distribution of eclosing apple and hawthorn adults, then the relative preference data from the field-release experiment predict that 32.9% of all flies on hawthorn trees should be of apple origin and 13.8% of flies on apple trees should be of hawthorn origin [32.9% = relative preference of apple-origin flies for hawthorn trees in the field-release experiment/(relative preference of apple-origin flies for hawthorn trees + relative preference of apple-origin flies for hawthorn trees) = 44.8%/(91.2% + 44.8%); 13.8% = 8.8%/(55.2% + 8.8%)]. Couple these host-preference differences with eclosing under the correct host species, as was the case for host-fidelity estimates derived from the switch experiment, and the percentage of interhost migrants on hawthorn trees would be reduced to 8.7% [7.9%/(83.3% + 7.9%)], while it would still be 15.3% [16.7%/(92.1% + 16.7%)] on apple trees. A significant interaction therefore exists for apple-origin flies between eclosing beneath apple trees and being genetically predisposed to accepting apples, an interaction that limits the movement of apple-origin flies to hawthorn trees. The same is not true for hawthorn-origin flies, however, suggesting that adult conditioning may only be pertinent for flies having the potential to accept alternative hosts. The 1992 net experiment indicates that 6.8% of all adults on hawthorn trees are apple-origin flies and 5.1% of the population on apple trees are hawthorn-origin flies [6.8% = percent recapture of apple-origin flies eclosing beneath apple trees on hawthorn trees in the net experiment/(total percentage of apple- and hawthorn-origin flies recaptured on hawthorn trees) = 6.9%/(95.0% + 6.9%); 5.1% = 5.0%/(93.1% + 5.0%)]. Therefore, host preference and eclosion origin cannot completely account for host fidelity, especially with regard to the hawthorn-infesting race. We will present data elsewhere showing that, because of the $\approx$10-day-later mean eclosion time of hawthorn-origin than apple-origin flies, allochronic isolation explains most of the remaining host fidelity. We also document that little ethological premating isolation exists between the races, as interracial matings between marked flies occurred at similar frequencies as intraracial crosses on both apple and hawthorn trees. In addition, we observed marked apple- and hawthorn-origin females ovipositing into apple and hawthorn fruits at statistically indistinguishable frequencies. Finally, genetic crosses suggest that postmating reproductive incompatibility is unlikely between apple- and hawthorn-origin flies (20). Consequently, our estimates of interhost movement based on the net study accurately reflect levels of genetic exchange between the races prior to any postmating selection.

In conclusion, our findings support the premise that host fidelity can be an effective premating isolating barrier. They also let us assign known reductions in gene flow between apple- and hawthorn-infesting races to the effects of specific host-associated traits related to host preference and adult eclosion. Seasonal differences in adult eclosion between the races underscore how host-associated adaptations can de-

velop and produce reproductive isolation as a correlated character (requirement *ii* for sympatric speciation). These differences in the timing of adult eclosion synchronize the life histories of apple- and hawthorn-origin flies with the fruiting phenologies of their respective host plants, while simultaneously causing allochronic mating isolation between the races as an indirect by-product. Differences in host phenologies may very well turn out to be essential for sympatric race formation and speciation in insects. Three of the best-studied cases for sympatric speciation, treehoppers in the genus *Enchenopa* (21–25), lacewings in the genus *Chrysoperla carnea* (26), and gall-forming Tephritids in the genus *Eurosta* (27) point to the interaction of insect development and host phenology as being a key consideration in population divergence.

The *Rhagoletis* story is not complete, however. The ≈6% level of genetic exchange between apple-origin and hawthorn-origin populations suggests that some as yet unidentified form of host-associated, postmating selection prevents fusion of the races. Our most likely candidate is tradeoffs in larval and pupal developmental rates imposed by differences in the fruiting phenologies of apples and hawthorns. This hypothesis remains to be tested, however. Furthermore, we must document whether and how additional reproductive isolation evolves between host races to complete the sympatric speciation process (requirement *iii* for sympatric speciation discussed in the Introduction). The existence of a number of sympatric and parapatric sibling species in the *R. pomonella* group, all of which are specialized on different sets of host plants, testifies that closure of the host race system is possible. But further work is required to determine the specific details of this aspect of sympatric speciation.

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